

Commentary

Resolving rapid dynamics of soil–plant–atmosphere interactions

Water is the main driver of ecosystem productivity in most terrestrial ecosystems worldwide. The predicted increase in rainfall variability and extreme climatic events under future climate conditions are therefore anticipated to strongly affect plant and ecosystem functioning. As 55–70% of terrestrial evapotranspirational water loss is directly controlled by plants (Schlesinger & Jasechko, 2014), transpiration comprises the largest water flux from Earth's continents, creating a dominant force in the global water cycle. Plant transpiration is controlled by the availability of soil water and root uptake from different soil depths, transport velocities in the xylem, and transpirational water loss through stomates during photosynthesis driven by the atmospheric demand (leaf-to-air water vapour deficit), and the species-specific sensitivity of stomatal control of water loss. In turn, plants modulate the available water resources in ecosystems by modifying interception, rain water infiltration, soil evaporation and groundwater recharge (e.g. Rodriguez-Iturbe, 2000). Different species with diverse rooting systems and depths have different effects on soil water infiltration, as well as different capacities to utilize various soil water pools (Jackson *et al.*, 2000). Since the 1980s, experimental evidence has ascertained the pivotal role of plant roots for soil water redistribution, such as hydraulic lift of deep water sources into shallower and dryer soil layers (Caldwell, 1987), thereby promoting or buffering competition for this highly valuable resource within plant communities. In spite of these insights, quantification of dynamic soil–vegetation feedbacks within the water cycle remains a major challenge. Progress has partially been hampered by the fact that blue (abiotic, e.g. stream, run off) and green (biotic, e.g. vegetation water losses) water flows were mostly investigated separately in different disciplines. Given that extreme events such as floods and droughts are predicted to increase in frequency for many regions, dynamic species-specific responses in root water uptake to changing available water pools play a pivotal role in the understanding of the ecosystem water balance and functioning. In this regard, more interdisciplinary approaches, bridging hydrology, ecophysiology and atmospheric science are needed. In this issue of *New Phytologist*, Volkmann *et al.* (pp. 839–849) were able to investigate this hidden part of the soil–vegetation interaction. Volkmann *et al.* quantified rapid dynamics of rainwater infiltration within the rooting zone of mixed and monoculture tree saplings. The consecutive responses in plant root water uptake and

utilization of a rain pulse revealed high species-specificities not in line with the distribution of roots within the soil profile. Furthermore, a novel dimension of temporal and spatial resolution in soil water flow processes was achieved, utilizing newly developed stable isotope-based methods.

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Water stable isotopes are a powerful tracer of water transfer in soils and at the soil–plant interface (Yakir & Sternberg, 2000; Werner *et al.*, 2012). Fractionation against the heavier isotopes occurring during phase changes (equilibrium fractionation) and movement (kinetic fractionation), result in measureable differences in stable hydrogen and oxygen isotope compositions ($\delta^2\text{H}$ and $\delta^{18}\text{O}$) in different source water pools (i.e. rain, groundwater), within the soil matrix, and subsequently in different plant species (Fig. 1). These differences provide vital insights into the terrestrial water cycle. For example, utilization of different water pools within the soil by different individual plants may be possible, and isotopes can help to separate transpiration from soil evaporative fluxes (Dubbart *et al.*, 2013). Over the last decade, the development of field-deployable laser spectroscopy has enabled continuous measurements of water vapour and its isotopic signatures in ecosystem fluxes and atmospheric concentrations, opening the door for large-scale assessment of the biosphere–atmosphere interactions in the water cycle. In particular, these developments have enhanced the spatial and temporal resolution tremendously, leading to new understanding in the fields of plant ecophysiology (Cernusak *et al.*, 2015) and ecosystem physiology (Dubbart *et al.*, 2014).

The isotopes $\delta^2\text{H}$ and $\delta^{18}\text{O}$ have also been used to study water movement in soils or at the soil–vegetation interface (Caldwell *et al.*, 1998). The $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of plant water uptake can be determined by sampling the 'output' of the root system, for example the plant xylem, because the water isotopic signatures are usually not altered by plant water uptake (Dawson, 1993). Compared with values observed in the soil water profile, the preferential plant extraction depth can be determined. Although this method has been successfully used to identify processes such as hydraulic lift and soil water redistribution (Caldwell *et al.*, 1998), classical destructive sampling techniques of soil and plant waters usually resulted in datasets with limited temporal and spatial resolution.

This article is a commentary on Volkmann *et al.*, 210: 839–849.

Recently, the development of membrane-based *in situ* methods of soil water sampling (Rothfuss *et al.*, 2013; Volkman & Weiler, 2014; Gaj *et al.*, 2016) has opened new avenues for assessing the dynamic changes in stable isotope composition of soil water sources, thus elucidating the fast dynamics in soil–vegetation

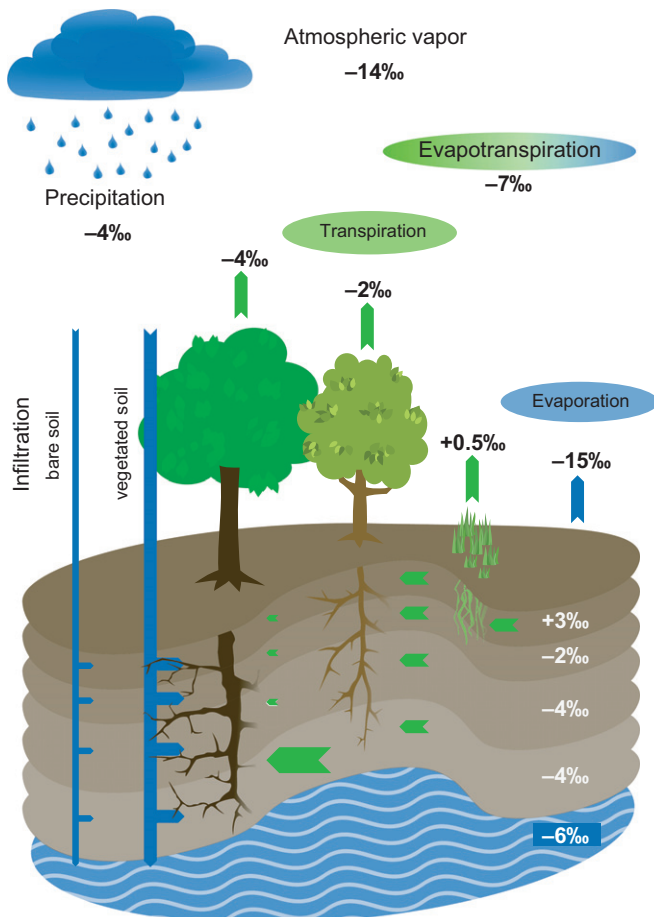


Fig. 1 Schematic overview on selected water flow paths through an ecosystem. Numbers denote oxygen isotope signatures (‰, values are approximations) of major water pools, thicker and lighter arrows denote different flow strength. Green and blue arrows symbolize biotic and abiotic water flow paths, respectively. © D. Dubbert.

interaction and its feedbacks on the hydrological cycle. Volkman *et al.* prove that linking these new methods with an artificial rain event highly enriched in the heavy isotopes, and plant chamber measurements, greatly improves our understanding of processes at the plant–soil hydrological interface. Comparing the vegetation response in monocultures and mixtures of sapling plantations of two different tree species (oak and beech) demonstrated a very distinct response of each species regarding the velocity and root water uptake pattern from different soil depths in response to the drought–rewetting event. Moreover, they nicely demonstrated that the dynamics and plasticity in root water uptake, which depend on, for example, water availability and plant community structure and interspecific interaction, was not necessarily in line with root density profiles (Fig. 2). Specifically, while one tree species (beech) exhibited a homogeneous root density distribution and uptake along the soil profile, the highest water uptake of oak saplings occurred at the lowest soil depth, that is, the layer with the lowest root density. This clearly contrasts with the common perception central to ecological, hydrological, and climate models that the uptake distribution is directly controlled by the root density distribution (Schymanski *et al.*, 2008). Thus, this is equivalent to the reasoning that the velocity of emptying a glass of water does not require a large number of drinking straws but is determined by the demand (i.e. the uptake velocity) of the person drinking it. In a similar manner, plants are able to meet their demands by regulating both the uptake depth from different soil layers and transport velocity within their conductive system in a dynamic and species-specific manner. In this regard, it is important to note that roots provide multiple functions beyond water uptake; for example tree stability and competition with neighbours for space and nutrients, the latter being generally more abundant in the upper soil horizons. Thus, the view that root density distribution will inform water uptake or partitioning, particularly considering the highly dynamic nature in space and time of this process, is a clear oversimplification. In agreement with Volkman *et al.*, we anticipate that the presented approach will help answer fundamental questions of the soil–vegetation–atmosphere interactions in the hydrological cycle, and promote research across disciplinary boundaries. Moreover, the dominance of plant control of transpiration water fluxes in continental evapotranspiration suggests that the next generation of climate models should prioritize

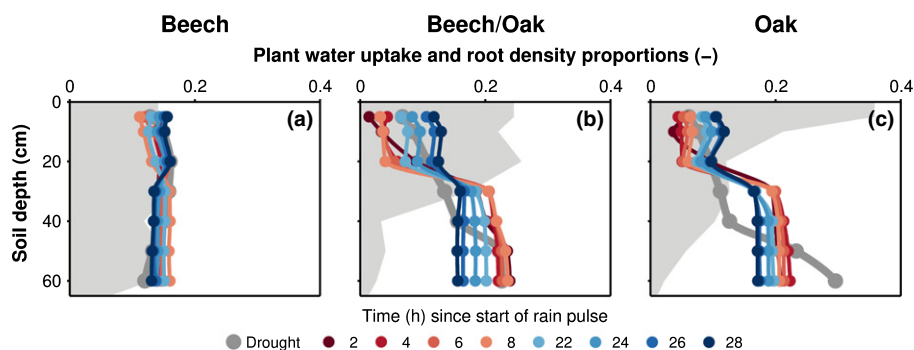


Fig. 2 Root distribution (grey shaded area) and depth distributions of water uptake (lines) at different times over the course of a rain pulse experiment along soil profiles under (a) beech monoculture, (b) mixed culture of beech and oak, and (c) oak seedlings monoculture. Markers and solid lines are means of root water uptake after a drought period (grey line) and time since start of the rain pulse (coloured lines, 2–28 h). Adapted from Volkman *et al.* in this issue of *New Phytologist* (pp. 839–849).

improvements in simulations of biological fluxes (Schlesinger & Jasechko, 2014).

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Christiane Werner* and Maren Dubbert

Department of Ecosystem Physiology, University Freiburg,
Georges-Köhler-Allee 53/54, Freiburg 79110, Germany

(*Author for correspondence: tel +49 761 2038303;
email c.werner@cep.uni-freiburg.de)

References

- Caldwell MM. 1987. Plant architecture and resource competition. In: Schulze E-D, Zwolfer H, eds. *Ecological studies, vol. 61*. Berlin/Heidelberg, Germany: Springer-Verlag, 164–179.
- Caldwell MM, Dawson TE, Richards JH. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* 113: 151–161.
- Cernusak LA, Barbour MM, Arndt SK, Cheesman AW, English NB, Feild TS, Helliker BR, Holloway-Phillips MM, Holtum J, Kahmen A *et al.* 2015. Stable isotopes in leaf water of terrestrial plants. *Plant, Cell & Environment*. doi: 10.1111/pce.12703.
- Dawson TE. 1993. Hydraulic lift and water-use by plants – implications for water-balance, performance and plant–plant interactions. *Oecologia* 95: 565–574.
- Dubbert M, Cuntz M, Piayda A, Maguás C, Werner C. 2013. Partitioning evapotranspiration – testing the Craig and Gordon model with field measurements of oxygen isotope ratios of evaporative fluxes. *Journal of Hydrology* 496: 142–153.
- Dubbert M, Piayda A, Cuntz M, Correia AC, Costa E Silva F, Pereira JS, Werner C. 2014. Stable oxygen isotope and flux partitioning demonstrates understory of an oak savanna contributes up to half of ecosystem carbon and water exchange. *Frontiers in Plant Science* 5: 530.
- Gaj M, Beyer M, Koeniger P, Wanke H, Hamutoko J, Himmelsbach T. 2016. *In-situ* unsaturated zone stable isotope (^2H and ^{18}O) measurements in semi-arid environments using tunable off-axis integrated cavity output spectroscopy. *Hydrology and Earth System Sciences* 20: 715–731.
- Jackson RB, Sperry JS, Dawson TE. 2000. Root water uptake and transport: using physiological processes in global predictions. *Trends in Plant Science* 5: 482–488.
- Rodriguez-Iturbe I. 2000. Ecohydrology: a hydrologic perspective of climate–soil–vegetation dynamics. *Water Resources Research* 36: 3–9.
- Rothfuss Y, Vereecken H, Brueggemann N. 2013. Monitoring water stable isotopic composition in soils using gas-permeable tubing and infrared laser absorption spectroscopy. *Water Resources Research* 49: 3747–3755.
- Schlesinger WH, Jasechko S. 2014. Transpiration in the global water cycle. *Agricultural and Forest Meteorology* 189: 115–117.
- Schymanski SJ, Roderick ML, Sivapalan M, Hutley LB, Beringer J. 2008. A canopy-scale test of the optimal water-use hypothesis. *Plant, Cell & Environment* 31: 97–111.
- Volkman THM, Haberer K, Gessler A, Weiler M. 2016. High-resolution isotope measurements resolve rapid ecohydrological dynamics at the soil–plant interface. *New Phytologist* 210: 839–849.
- Volkman THM, Weiler M. 2014. Continual *in situ* monitoring of pore water stable isotopes in the subsurface. *Hydrology and Earth System Sciences* 18: 1819–1833.
- Werner C, Schnyder H, Cuntz M, Keitel C, Zeeman MJ, Dawson TE, Badeck FW, Bruognoli E, Ghashghaie J, Grams TEE *et al.* 2012. Progress and challenges in using stable isotopes to trace plant carbon and water relations across scales. *Biogeosciences* 9: 3083–3111.
- Yakir D, Sternberg LDL. 2000. The use of stable isotopes to study ecosystem gas exchange. *Oecologia* 123: 297–311.

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